Chapter 7
The Influence of Environmental Factors on Earthworms

Earthworms are thin-skinned invertebrates with little protection against the changes in moisture and temperature that occur in soils or the physical and chemical characteristics such as soil type, pH, porosity, and organic matter content of the soils in which they live. Some environmental components such as soil pH, moisture, and temperatures are some of the pressures that dictate earthworm movement and development. Earthworms have been demonstrated to be sensitive to a range of these environmental pressures and have shown certain relationships to them in addition to biodiversity and soil functioning (Leveque et al., 2015; Rutgers et al., 2016).

7.1 Moisture

Water constitutes 75–90% of the body weight of earthworms (Grant, 1955a), so prevention of water loss is a major factor in earthworm survival. Generally, low moisture is detrimental to earthworm growth (Berry & Jordan, 2001; Baker & Whitby, 2003a, b). Nevertheless, they have considerable ability to survive adverse moisture conditions, either by moving to an area with more moisture or by estivating. If they cannot avoid dry soil, they can still survive the loss of a large part of the total water content of their bodies. For instance, *L. terrestris* can lose 70% and *A. chlorotica* 75% of their total body water and still survive (Roots, 1956). Grant (1955a) considered that most lumbricid worms could sustain a water loss of at least 50%. Earthworms apparently lack a mechanism to maintain a constant internal water content, so that their water content is influenced greatly by the water potential of the soil (Kretzschmar & Bruchou, 1991).

Earthworm activity also depends upon adequate availability of soil moisture, but not all species have the same moisture requirements, and, within a species, the moisture requirements for earthworm populations from different regions of the world can be quite different. For example, in Europe, *A. caliginosa* goes into

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diapause at a soil moisture content below 25–30% and does not survive well below 20% soil moisture (Baltzer, 1955), whereas in seasonally arid regions of Argentina, *A. caliginosa* and *A. rosea* are active in soils with moisture content as low as 15% (Ljungström & Emiliani, 1971; Ljungström et al., 1973). Buckerfield (1992) reported that populations of *A. trapezoides* and *A. rosea* were still active at soil moisture contents as low as 10%, in cereal fields of the semiarid region of southern Australia. Such results indicate that certain peregrine species are capable of adapting to a wide range of moisture conditions.

The moisture preferences of only a few earthworm species have been determined experimentally. Madge (1969) placed earthworms of the species *H. africanus* in moisture gradients and reported that they preferred soil between 12.5% and 17.2% moisture content. Soil with a moisture content of about 23.3% appeared to be optimal for them to produce casts. *Allolobophora caliginosa* and *Metaphire californica* seemed to prefer soil moisture contents of 20–45% and 35–55%, respectively, in clay soil (El-Duweini & Ghabbour, 1968). The preference of *M. californica* for wetter soils may be due to the fact that it is not as tolerant of desiccation as *A. caliginosa* (Ghabbour, 1975), and the same may be true for *L. rubellus*. Earthworms that live in compost or dung heaps tend to prefer moisture conditions than most species of soil-dwelling earthworms. For instance, juvenile and adult *P. excavatus* preferred a moisture content of around 80% in cattle manure at 25 °C (Hallett et al., 1992) and 80–85% in other organic materials (Edwards, 1988). The growth, fecundity, and mortality of the epigeic earthworm *Eisenia fetida* in cattle manure solids and pig manure solids with different moisture contents (70%, 75%, 80%, 85%, 90%) were studied for 30 weeks in the laboratory (Gunadi et al., 2003). The maximum weight of *E. fetida* in the pig manure solids, which had a moisture content of 75%, was 1100 mg after 13 weeks with a highest growth rate of 12.8 mg d^{-1}. The total number of cocoons and hatchlings produced was lower, compared to those in all the other moisture levels. Generally, earthworms grew bigger and faster in pig manure solids than in separated cattle manure solids, but the mortality at all moisture levels in pig manure solids was high, ranging from 20% to 100% (Figs. 7.1 and 7.2)

To determine the most favorable moisture condition for *E. andrei*, a species closely related to *E. fetida* that are used to process organic wastes commercially, Dominguez and Edwards (1997) found that 85% moisture, in a media made up of pig manure, was the most favorable in promoting growth and maturation (Fig. 7.3).

Clearly, maximum growth was achieved at 85% moisture level, and maturation was achieved at moisture levels greater than 85% up to 90% (Table 7.1)

Prolonged droughts decrease numbers of earthworms markedly, and it may take as long as 2 years for populations to recover once conditions become favorable again. One important factor seems to be that the fecundity of earthworms such as *A. chlorotica* is influenced greatly by moisture (Table 7.2). Gerard (1960) showed that some species can withstand dry conditions much better than others; for instance, *L. terrestris* survived as well in non-irrigated plots as in irrigated ones, whereas *A. chlorotica*, *A. caliginosa*, and *A. rosea* did not survive in non-irrigated plots.

Earthworms that migrate to deeper soil when the surface soil is too dry include *L. terrestris*, *A. longa*, *E. fetida*, and *P. hupeiensis*. Despite not migrating to deeper

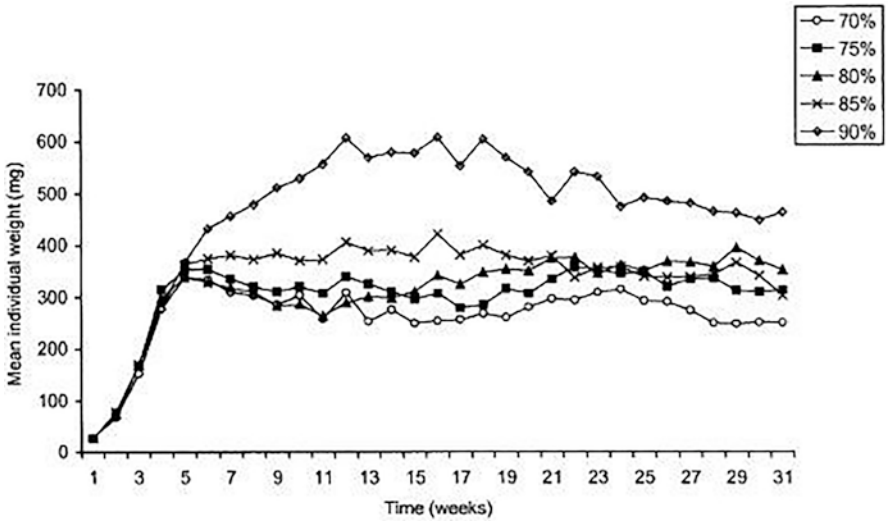

Fig. 7.1 The rates of growth of *Eisenia fetida* in cattle manure solids with different moisture contents over 30 weeks

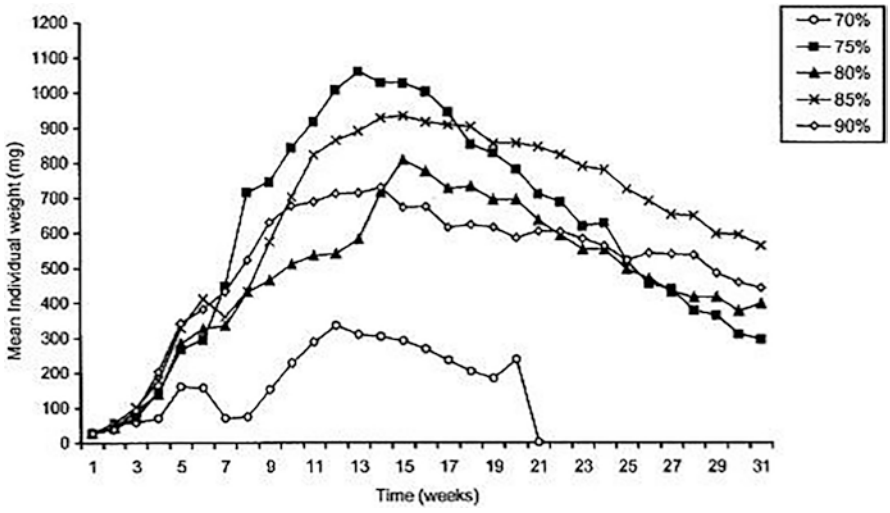

Fig. 7.2 The rates of growth of *Eisenia fetida* in pig manure solids with different moisture contents over 30 weeks

soil, *A. caliginosa* is usually considered able to survive very dry conditions, in spite of Gerard's conclusions (1960), but *Octolasion lacteum* is not (Grant, 1955a). Lack of moisture can cause some earthworm species to become quiescent or go into diapause. For instance, *Aporrectodea* spp. are active in the upper 10 cm of soil when the soil is moist, but when the soil is dry, they are usually found below 20 cm, where

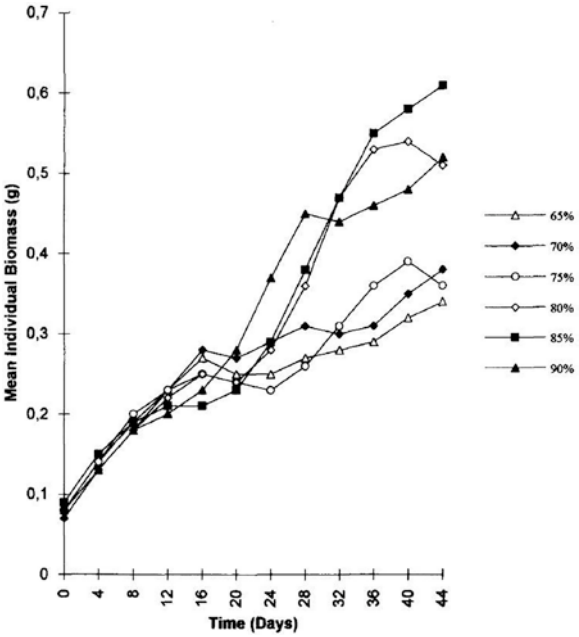

Fig. 7.3 Growth of *E. andrei* on a pig manure moisture at different moisture contents over 44 days at 20 °C

Table 7.1 Growth and maturation of *E. andrei* in pig manure at different moisture contents

Moisture content (%)	Growth rate (mg biomass d^{-1})	Max. indiv. biomass (mg) ± SD	Mean. indiv. biomass (mg) ± SD
65	5.80	335 ± 72 a[j]	268 ± 12 a
70	7.02	379 ± 90 a	295 ± 15 a
75	7.77	391 ± 90 a	304 ± 12 a
80	11.47	537 ± 162 b	467 36 b
85	11.81	608 ± 181 c	468 ± 31 b
90	9.93	515 ± 149 b*	449 ± 46 b

[j]Means in the same column followed by different letters are significantly different at $P \leq 0.01$ (ANOVA and Fisher LSD multiple comparison test)
*$P \leq 0.05$

they estivate, tightly coiled within spherical, mucus-lined cells (Lee, 1985; Baker et al., 1992). When individuals of *A. caliginosa* were kept in soil that was dried slowly in the laboratory, they went into diapause, but when kept in moist soil, they remained active for 18 months (Gerard, 1960). Kretzschmar and Bruchou (1991) subjected *A. longa* to constant levels of soil water suction and reported that a water suction level below −35.5 kPa caused water loss from the earthworms, and levels below −620 kPa led to diapause.

The effects of decreasing soil water potential on cocoon production, cocoon development, and growth of juveniles were investigated in the earthworm *Aporrectodea caliginosa* (Holmstrup, 2001). The earthworms were subjected to water potentials between 22 and ca. 2300 kPa, using two soil types with various

Table 7.2 The effect of soil moisture on cocoon production by *A. chlorotica*

Site	Bones close						
Moisture content of soil (%)	11	13.5	21	28	35.5	42.5	SE of difference
Mean no. of cocoons produced by five worms	0	0	8.6	13.6	8.8	6.6	0.94
Site	Westfield						
Moisture content of soil (%)		1.6	24.5	33	42	50	SE of difference
Mean no. of cocoons produced by five worms		0	0.6	8.4	9.4	3.0	0.93

From Evans and Guild (1948)

wetness. The duration of the drought exposure was 14 days, whereafter the earthworms were returned to ideal moisture conditions. Cocoon production was negatively affected when the water potential was lower than 212 kPa, and below 240 kPa cocoon production was completely arrested. The negative effect on cocoon production persisted for at least 2 weeks after the worms were moved back to soil with optimal moisture conditions. For those worms that were exposed to the most severe drought level, 2330 kPa, cocoon production was still significantly impaired 2 months after drought exposure. Juvenile growth was sensitive to decreasing water potential. Even at 26 kPa, the growth of juveniles was significantly lower than in controls, and at ca. 220 kPa, there was no growth at all. Cocoon development was less sensitive to water potential than growth and cocoon production. Thus, development seemed not to be affected by a 14-day exposure at water potentials above ca. 2700 kPa, whereas at higher levels, there was an increasing effect. When cocoons were exposed to ca. 23 MPa, the development was immediately arrested.

Parmelee and Crossley (1988) and Edwards et al. (1995) suggested that cocoons may act as the main survival stage during drought for some earthworm species, such as *L. rubellus*. Parmelee and Crossley reported that cocoon biomass increased as drought severity increased during a severe drought in a no-tillage agroecosystem on the Georgia Piedmont, USA, and that there were many small, immature earthworms of this species immediately following the drought.

Soil moisture can influence the numbers and biomass of earthworms at any given location. Olson (1928) surveyed areas of Ohio, USA, for earthworms and reported that the largest numbers of earthworms occurred in soils containing between 12% and 30% moisture. El-Duweini and Ghabbour (1965a), who investigated the survival of *A. caliginosa* in relation to soil moisture content in Egypt, reported that in soils with 5–85% gravel and sand, an increase in moisture content of from 15% to 34% was associated with an increase in numbers of *A. caliginosa*, but above 34% extra moisture had no effect. Wood (1974) showed that there was a strong positive correlation between earthworm biomass and increased soil moisture content for topsoil-inhabiting earthworm species surveyed at 18 different sites on Mt. Kosciusko

in southeastern Australia. Walsh et al. (2019) confirmed that soil moisture was significantly correlated to earthworm biomass and density.

Topography can also influence soil moisture where lower elevations would usually contain more moisture and would therefore favor earthworm habitation. Soil fauna, including earthworms, were found to populate on the bottom of all ravines considered in a transect sampling from sandstone massifs with different microclimates, than in upper elevations which ranges from 56 to 163 ind/m^2 (Schlaghamersky et al., 2014). Mesocosm studies suggested that drought was the main factor influencing retarding the litter mass loss across European agroecosystems irrespective of management types (da Silva et al., 2020). The study further indicated that functional diversity of earthworms was adversely affected by drought and eventually decreased little mass loss.

Most earthworms are more active in moist soils than dry ones, and during periods of considerable rain individuals of some species, such as *L. terrestris* come out on to the soil surface at night. The activity of a West African species, *Millsonia anomala*, which normally lives in the top 10 cm of soil, depends mainly on soil moisture. When moisture is inadequate, these earthworms go into dormancy and even die under extreme drought conditions. When the soil moisture content rises to 8–10%, surviving worms become active again, with 10–17% soil moisture being optimal; above this, moisture content conditions are often unsatisfactory (Lavelle et al., 1974). Abundance of *Amynthas agrestis* in hardwood forests did not show any correlation to moisture at all (Gorres et al., 2016)

Some workers would argue that movements of earthworms in soil are governed by soil water energy (matric suction) rather than soil wetness (moisture content). Doube and Styan (1996) reported that for *Aporrectodea rosea*, the threshold soil moisture level at which earthworms were induced to move away from dry soil, was a matric suction of about 300 kPa (pF 3.4) and was independent of soil type. In contrast, for *A. trapezoides*, the threshold soil moisture varied with soil type (sandy loam 15 kPa, loam 25 kPa, clay 300 kPa). They concluded that, for the earthworm *A. rosea*, matric suction and not water content of soil provided the cue by which the earthworm recognized dry soil. For *A. trapezoides*, there was an interaction between matric suction and soil type in which the response of *A. trapezoids* to soil moisture varied with soft texture and the threshold for avoidance of dry soil ranged from a matric suction of 300 kPa (20% w/w) in clay to 15 kPa (10% w/w) in sandy loam.

Soil moisture and temperature can act synergistically to influence earthworm activity. For example, Scheu (1987) showed that an increase in temperature from 10 to 15 °C, at 60% water content, doubled the numbers of casts produced by *A. caliginosa*, whereas at 48% water content, increasing the temperature to 15 °C increased cast production by only 20%. At 15 °C, an increase in water content from 48% to 60% caused a doubling of cast production. Using the same species, Eriksen-Hamel and Whalen (2006) showed that the instantaneous growth rate (IGR) of *A. caliginosa* is affected by the interaction between soil moisture (expressed as water potential) and temperature using undisturbed and disturbed field soils. Optimum growth conditions for *A. caliginosa* were at 20 °C and _5kPa water potential, and they lost weight when the soil water potential was _54 kPa for all temperatures and also when

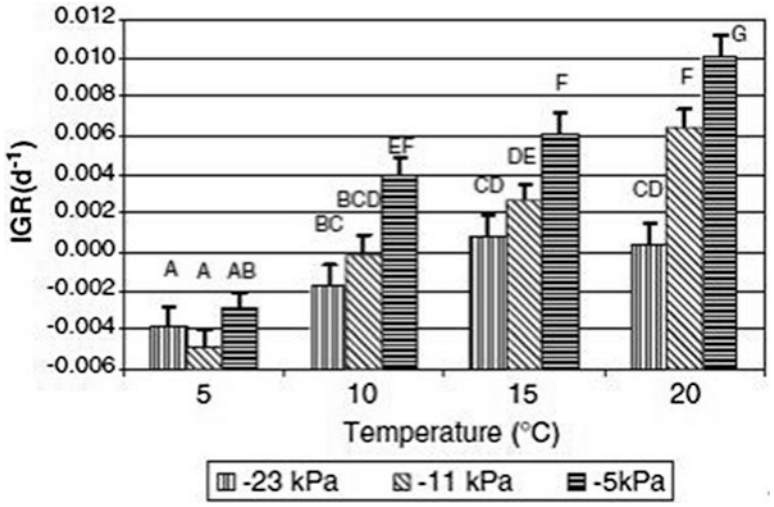

Fig. 7.4 Influences of soil temperature and moisture on the instantaneous growth rate (IGR) of A caliginosa in pots. Values shown as means ± SE (n =10). Columns with the same letters did not differ significantly

the temperature was 5 °C for all water potentials. Growth rates were significantly greater in pots than in cores, but the growth rates of earthworms in cores with undisturbed or disturbed soil did not differ significantly (Fig. 7.4)

Wever et al. (2001) examined the combined influence of soil moisture and temperature on survival, growth, and development of *Aporrectodea tuberculata*, a species common to the agricultural fields in the Canadian prairies. Soil moisture accounted for 48% of the variation in earthworm survival with the lowest survival associated with 10% soil moistures. The interaction terms, time × temperature × moisture, and time × temperature, accounted for 63% of the variation in earthworm growth. The greatest increase in earthworm weight was in soil incubated with 25% moisture at 15 and 20 °C. There was also an obvious relationship between survival and growth linked to the interaction between soil temperature and moisture. After 10 weeks, the only post-clitellate individuals were observed in the 25% and 20 °C treatment. Clitellate earthworms weighed 1.5 times more than individuals having only genital tumescences (GT). The results of the study showed that the effects of soil moisture on earthworm growth and survival are modified by soil temperature. Using thermal time and hydrotime models for predicting growth and development of temperate earthworms, Moreau-Valancogne et al. (2013) described three cardinal temperatures, namely, base temperature (T_b), optimal temperatures (T_o), and ceiling temperatures (T_c). The model predicted the Tb values of 4.3 °C and 2.5 °C, To values at 21.2 °C and 17.6 °C, and Tc values of 38.1 °C and 25.8 °C for cocoon development and growth, respectively. The model also demonstrated that at constant temperature, cocoon development and growth decreased linearly with water potential, as described by the hydrotime model. Base water potential (the water potential

at which life history parameter values are zero) was found to be close to very wet conditions for growth (−23 and −10 kPa for juveniles and adults, respectively) and cocoon production (−32 kPa).

El-Duweini and Ghabbour (1968) compared two species, *A. caliginosa* and P. *californica*, for their ability to resist desiccation and showed that *A. caliginosa* could resist desiccation, but *P. californica* could not, preferring soil moisture levels just below the waterlogging levels. These differences could be related to the relative efficiency of water discharge via the earthworms' nephridia. Ayres and Guerra (1981) compared the ability of different earthworms from the central Amazon to withstand desiccation. They showed that *Pontoscolex corethrurus*, a species that inhabits soils with a wide range of moisture content, was much more resistant to dehydration than were two other species, *Androrrhinus caudatus* and *Meroscolex marcusiz*, which inhabit only moist soils.

Many species of earthworms can survive long periods submerged in water. For instance, *A. chlorotica*, *A. longa*, *D. subrubicunda*, *L. rubellus*, and *L. terrestris* were all able to survive from 31 to 50 weeks in soil totally submerged below aerated water (Madge, 1969). *Allolobophora caliginosa* was also able to survive for 10–20 weeks in aerated water without food; H. *africanus* could survive for more than 9 weeks submerged. The main problem during submergence is the uptake of water into the worm, but most species have adequate means of overcoming this, although they depend on maintenance of oxygenation in the water (Chap. 4). Cocoons can hatch underwater, and the young worms can feed and grow for a time although totally immersed (Roots, 1956). Some earthworms, such as the North American species *Sparganophilus eiseni*, are semiaquatic and spend most of their life cycle submerged (Harman, 1965). Zorn et al. (2008) studied the responses of three earthworm species, *Allolobophora chlorotica*, *Aporrectodea caliginosa*, and *Lumbricus rubellus* to flooding experiments. *A. chlorotica* was tolerant to water, although the worms tended to escape from flooded soil. Their health was significantly lower in the flooded soils ($P < 0.05$). *A. caliginosa* showed little response to flooding. *L. rubellus* was sensitive toward flooding, with escape and avoidance behavior being the main mechanism of survival. This species was able to survive when forced to stay in flooded soil for at least 42 days, but this significantly reduced its health ($P < 0.05$). On the other hand, Kiss et al. (2021a, b) reported that earthworm abundance in the crop and pasture soils and total earthworm biomass in the crop soils was significantly lower in the frequently flooded areas than in the rarely flooded areas. The relative percentage difference in the populations between the rarely and frequently flooded areas was greater in the crop soils (−59.18% abundance, −63.49% biomass) than the pasture soils (−13.39% abundance, −9.66% biomass).

The ability of soil animals, especially earthworms, to survive flooding depends on their behavioral, morphological, and physiological properties. Earthworms and insect larvae dispose of the entire spectrum of strategies to survive flooding including horizontal and vertical migration, physiological adaptation, as well as phenology and reproduction strategies.

Martay and Pearce-Higgins (2018) modeled the variation in soil invertebrates across the United Kingdom using factors such as weather, climate, season, and habitat. They found that the abundance and biomass of earthworms were strongly correlated with soil moisture.

7.2 Temperature

The activity, metabolism, growth, respiration, and reproduction of earthworms are all influenced greatly by temperature. Temperature also influences food consumption by earthworms (Daniel, 1991; Daniel et al. 1996a, b). Temperature and moisture are usually inversely related, and high surface temperatures and dry soils are much more limiting to earthworms than low temperatures and waterlogged soils (Nordström & Rundgren, 1974).

Weight gain and loss, maturation time, and mortality of juvenile populations of *L. terrestris* were investigated in the laboratory by Daniel et al. (1996a, b) exposed to temperatures ranging from 7.5 to 25 °C. *L. terrestris* increased faster at temperatures at intermediate rather low and high temperatures when fed ad libitum with dandelion for 8 weeks. Weight gain ranged from 0.8 g (7.5 °C) to more than 1.8 g (17.5 °C) (Fig. 7.5).

However, the incipience of male pores and the development of clitellum were not temperature dependent. The duration from hatching until the development of male pores was 25.7 weeks at 7.5 °C and 9.4 weeks at 20 °C. The additional time needed for the development of clitellum was 4.7 and 2, 3 weeks, respectively.>?, "<

Fecundity is affected very much by different temperatures. For instance, the numbers of cocoons produced by *A. caliginosa* and certain other lumbricid species were reported to quadruple over the range from 6 to 16 °C (Evans & Guild, 1948). The optimum temperature for cocoon production by *L. terrestris* was 15 °C with 25.3 cocoons produced per annum (Butt, 1991). Cocoons also tend to hatch sooner at higher temperatures; for example, cocoons of *A. chlorotica* hatched in 36 days at 20 °C, 49 days at 15 °C, and 112 days at 10 °C when there was adequate moisture (Gerard, 1960). Cocoons of *L. terrestris* hatched more rapidly at 20 °C than at other temperatures (Butt, 1991). However, there may be an inverse relationship between the percentage hatch of cocoons and temperature. Cocoon production by *E. fetida* increased linearly with increases in temperature from 10 to 25 °C, although the number of hatchlings per cocoon was lower at 25 than at 20 °C (Reinecke & Kriel, 1981). When *Dendrobaena octaedra* populations were raised in constant temperatures, 15 ± 0.5 °C for 47 weeks, cocoon production was seasonal (Rozen, 2006). Cocoon production increases during spring and summer and decreases in winter suggesting that cocoon production is controlled by some internal mechanisms by earthworms.

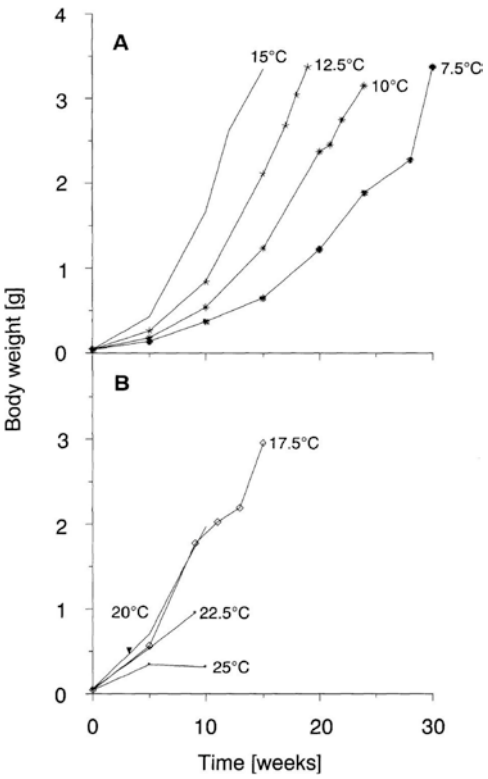

Fig. 7.5 Weight gain of L.terrestris fed ad libitum with dandelion leaves ar various temperatures: (A) temperature ≤ 15 °C (mortality up to maturity = 0) (B) temperature 15 °C (mortality up to maturity ≥ 0)

The duration of incubation time in relation to ambient temperature was measured for cocoons of four lumbricid earthworm species (Holmstrup et al., 1991). Cocoons were obtained from laboratory cultures of *A. caliginosa*, *A. rosea*, *A. chlorotica*, and *D. octaedra*. The cocoons were incubated at 5, 10, 15, and 20 °C at optimum moisture conditions. Incubation time increased greatly with decreasing temperature, but embryonic development took place at all four experimental temperatures. Cocoons of *A. caliginosa*, *A. rosea*, and *A. chlorotica* developed within 34–38 days at 20 °C and within 59–66 days at 15 °C. *Dendrobaena octaedra* cocoons developed within 47 days at 20 °C and 92 days at 15 °C. At 10 °C, *A. caliginosa* had the shortest cocoon incubation time, followed by those of *A. rosea*, *A. chlorotica*, and *D. octaedra*. At 5 °C, *A. chlorotica* and *D. octaedra* cocoons developed for about 400 days, whereas those of *A. caliginosa* needed only about 230 days. It is suggested that a lower threshold temperature for cocoon hatching exists for most earthworm species but that embryonic development can still take place even though temperature is below this threshold. The ability of the embryo to develop at low temperatures should be regarded as an adaptation to the particular habitat in which the species is living, making it possible for the juveniles to emerge as soon as environmental conditions are favorable.

The growth period from hatching to sexual maturity is also dependent on temperature; for instance, *A. chlorotica* took 29–42 weeks to mature in an unheated cellar (Evans & Guild, 1948), 17–19 weeks at 15 °C (Graff, 1953), and only 13 weeks at 18 °C (Michon, 1954). *Eisenia fetida* took *9½* weeks to mature at 18 °C and only 6½ weeks at 28 °C (Michon, 1954). Viljoen et al. (1992) reported that *D. veneta* completed its life cycle in 107 days at 15 °C and in 151 days at 25 °C. However, the hatching success and the number of hatchlings emerging per cocoon were greater at the lower temperature, which was more characteristic of the earthworm's natural habitat in Europe. Experiments in England on the intensive culturing of *L. terrestris* at various temperatures showed that cocoon production was greatest at 15 °C, and the length of cocoon incubation was shortest at 20 °C, with the ideal temperature for maximum production falling within the range of 15–20 °C (Butt, 1991). The temperature at which earthworms thrive best and which they prefer is not necessarily the same as that at which they grow fastest or are most active.

Lee (1985) reported that the optimal temperature for growth of indigenous populations of Lumbricidae in Europe ranges from 10 to 15 °C. Daughberger (1988) verified these temperature optima in laboratory experiments, in which he showed that the temperature preference of *L. terrestris* was 10 °C and that of both *A. caliginosa* and A. *longa* was between 10 and 15 °C. *Dendrobaena rubida*, which inhabits litter, and *L. rubellus*, which lives close to the soil surface, have temperature optima in the range of 15–20 °C. Some species of earthworms that inhabit compost or dung heaps have temperature optima closer to 25 °C (Edwards, 1988). Grant (1955b) showed that the temperature preferendum was 15–23 °C for *P. hupeiensis*, 15.7–23.2 °C for *E. fetida*, and 10–23.2 °C for *A. caliginosa*. *Eisenia rosea* preferred temperatures between 24.1 and 25.6 °C (Reinecke, 1974).

Kollmannsperger (1955) reported that the number of lumbricid earthworms found on the soil surface at night was correlated positively with temperature and that the optimum temperature for activity was 10.5 °C. Satchell (1967) concluded that the most suitable conditions for activity of earthworms on the surface were nights when soil temperatures did not exceed 10.5°C, grass-air temperatures were above 2 °C, and there had been some rain during the previous 4 days. These optima have been used to identify the best nights to collect *L. terrestris* for fish bait in Canada (Tomlin, 1983). Graff 1953) listed the optimum temperatures for development of lumbricids (Table 7.3).

European lumbricids introduced and established in warmer climates can have different temperature optima than representatives of the same species in Europe. For example, the optimum temperature for *A. rosea* was reported to be around 25 °C in laboratory experiments in South Africa (Reinecke, 1975) but was reported to be 12 °C for field populations of earthworms in Germany (Graff, 1953). Tropical earthworm species tend to have higher temperature optima than species from temperate regions (Lee, 1985).

Few unmanaged soils in Walker County, southeastern Texas, are colonized by earthworms. Mixed oak-savannah and pine forest occur in acidic sands that comprise 86% of the 2049 km^2 total surface area in Walker County. These acidic sands

Table 7.3 Optimum temperatures (°C) for the development of earthworms

A. rosea	12
A. caliginosa	12
A. chlorotica	15
O. cyaneum	15
L. rubellus	15–18
D. attemsi	18–20
D. rubida	18–20
E. fetida	25

From Graff (1953)

are not suitable habitat for earthworms but have reported to have been colonized seasonally by two species of *Diplocardia*: *Diplocardia invecta* and *Amynthas corticis* (syn. *Amynthas diffringens*) (Millican & Lutterschmidt, 2007). It was further reported that at soil temperatures from 8 to 26 °C, *D. invecta* and *A. corticis* each remained active. When surface temperature was 26 °C and moisture was 80% saturation, *D. invecta* was not observed at the surface. If *D. invecta* could not burrow to depths where temperature was 28 °C, it became quiescent, or inactive, at depths of 20–30 cm.

Earthworms can be killed by temperatures outside their survival limits. For instance, it has been suggested that earthworm populations in arable soils in the United States can be destroyed by frost in the absence of ground cover (Hopp, 1947), but in pasture or woodlands, it is unlikely that the soil would freeze deeply enough to affect populations of most species.

The upper lethal temperature for earthworms is lower than for many other invertebrates, although there is considerable variation in estimates of these temperatures by different workers. For instance, El-Duweini and Ghabbour (1965b) reported median upper lethal temperatures of 37.037.75 °C for *Pheretima californica* and 39.55–40.75 °C for *A. caliginosa* after only 30 min exposure. Other workers have reported much lower upper lethal temperatures after 48 h exposure, such as 28 °C for *L. terrestris*, 26 °C for *A. caliginosa*, 25 °C for *E. fetida*, 25 °C for *P. hupeiensis* (Grant, 1955b), and 29.7 °C for *A. rosea* (Reinecke, 1974). Such temperatures can occur in field soils in many areas in which these species live. El-Duweini and Ghabbour (1965b) determined the preferred and lethal temperatures for *P. californica* and a species of *Alma* (Fig. 7.6). The preferred temperatures for these species were 26–35 °C and 24–26 °C, respectively, and the upper lethal temperatures 37 °C and 38 °C, respectively. Worms could survive the higher temperatures much better in air than in soil.

More recently, Berry and Jordan (2001) reported that 30 °C were fatal to *L. terrestris* after 14 days and 25 °C after 182 days.

The lower lethal temperatures for earthworms from temperate regions are apparently close to the freezing point. Earthworms are known to survive in surface soils that are frozen in winter, and it is likely that species from extremely cold habitats

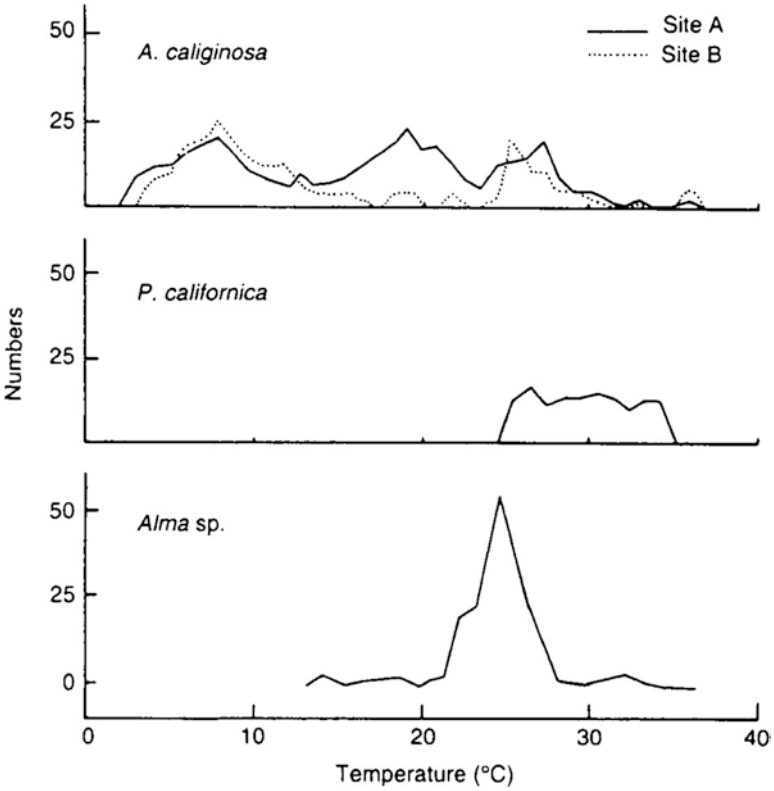

Fig. 7.6 Temperature preferences of *A. caliginosa, P. califomica* and *Alma sp*. (after El-Duweini and Ghabbour, 1965b)

possess some capacity to tolerate cold or resist freezing of their tissues. However, neither *A. caliginosa* nor *E. fetida* survived exposure to 0 °C for 48 h in the laboratory (Grant, 1955b). Schmidt (1918) reported that *E. fetida* had a lower lethal temperature limit of −1.3–2.0 °C, indicating only a limited capacity for this species to endure freezing conditions. Bodenheimer (1935) reported a similar lower limit (−1.3 °C) for *Bimastos samerigera* in Israel. It has been claimed that *Eisenia nordenskioeldi* in Russia can survive long periods of being entirely frozen (Lee, 1985). The lower thermal death point of the tropical earthworm *H. africanus* was reported to be 7.5 °C, which is well below temperatures that this species encounters in its natural tropical environment. Cocoons of earthworms that inhabit extremely cold environments have been shown to survive freezing temperatures (Holmstrup et al., 1990; Holmstrup, 1994). Holmstrup (1994) investigated the cold hardiness of five earthworm taxa (*D. octaedra*, *D. rubidus tenuis*, *D. rubidus norvegicus*, *A. caliginosa*, and *A. chlorotica)* and showed that *D. octaedra* was the most cold hardy, being able to survive at −8 °C for 3 months and −13.5 °C for 2 weeks in frozen soil.

Earthworm cocoons are apparently not freeze-tolerant, but rather their cold-hardiness strategy is to become extremely desiccated to prevent freezing of their tissues in frozen environments.

Earthworms are capable of acclimatizing to different temperatures. Grant (1955b) studied the effect of conditioning temperatures on the upper lethal levels of temperature for *P. hupeiensis*. Earthworms of this species conditioned at 4 °C, 9 °C, and 15 °C had thermal death points of 19.4 °C, 20.9 °C, and 22.7 °C, with an average gain in heat tolerance of 0.3 °C for every 1 °C rise in conditioning temperature, up to an upper limit of about 25 °C. Earthworms kept at 15 °C took 12 days to acclimatize to a new environmental temperature of 22 °C. Such mechanisms allow gradual adjustment to seasonal changes in temperature. Earthworms may have some limited capacity to cool themselves by evaporating water from the surface of their bodies, but this is effective only at high soil water potentials when the risk of desiccation is low (Hogben & Kirk, 1944). A more recent study reported that earthworms (Siebert et al., 2019) can modulate the effects of climate warming, with declining populations, and in turn interactively affect soil biota. The same study concluded that under elevated temperature, earthworm structures become particularly important for species to find shelter and avoid adverse soil conditions like water shortage.

Earthworms can migrate away from soil at unsuitable temperatures; in experiments in which individuals of *A. caliginosa* could choose between soils at different temperatures, they preferred soil from 10 to 23 °C, and individuals of *E. fetida* preferred soils from 16 to 23 °C (Grant, 1955b). Dowdy (1944) reported that *Diplocardia* sp. moved down to lower soil strata at temperatures below 6 °C. Madge (1969), who tested species of *H. africanus* in a temperature gradient, found that they aggregated between 23.9 and 31.5 °C and avoided temperatures above 34 °C. These temperatures are higher than those at which most other worms can survive, but this is a tropical species, which must tolerate high temperatures to be able to survive in its environment.

Gorres et al. (2016) reported that *Amynthas agrestis*, an invasive species in the hardwood forest in the Chaplain Valley, Vermont, started dying off below 5 °C, and hatchings were observed at air temperature reached above 10 °C. This confirmed earlier experiments by Richardson et al. (2009) who reported that there was 100% mortality of *A. agrestis* at temperatures lower than 5 °C and that cocoons hatched at temperatures greater than 10 °C (Blackmon, 2009). However, it seems like larger *A. agrestis* survived temperatures in colder temperatures (Gorres et al., 2016) and cocoons can survive soil temperatures below −20 °C.

Temperature also affects the numbers of leaves buried by *L. terrestris*, which can be used as an index of earthworm activity in relation to temperature (Edwards & Lofty, 1977). Daniel (1991) expressed the consumption of dandelion leaves by *L. terrestris* as a function of temperature and moisture. He reported that food consumption of this species increased linearly with temperature up to 20°C but declined above 22°C and declined linearly with decreases in soil water potential below –7.0 kPa.

Daniel et al. (1996a, b) studied the cast production of *A. nocturna* as affected by different temperatures among other soil factors.

7.3 pH

It has been demonstrated that earthworms are very sensitive to the hydrogen ion concentration (pH) of aqueous solutions (Chap. 4), so it is not surprising that soil pH is sometimes a factor that limits the species, numbers, and distribution of earthworms that live in any particular soil. Some species are intolerant of acid soil conditions, whereas others thrive under acid conditions, and many species can tolerate a wide range of pH. It has been demonstrated that generally, soils with lower pH do not favor earthworm growth and development (Berry & Jordan, 2001; Baker & Whitby, 2003a, b). Divergent genetic lineage of *L. rubellus* has shown to have positive correlation with soil pH (Spurgeon et al., 2016).

Several workers have stated that most species of earthworms prefer soils with a neutral pH (pH = 7.0) (Arrhenius, 1921; Moore, 1922; Phillips, 1923; Salisbury, 1925; Allee el al., 1930; Bodenheimer, 1935; Petrov, 1946). However, *L. terrestris* occurs in soils with a pH of 5.4 in Ohio, USA (Olson, 1928), and *A. caliginosa* in soils with a pH of 5.2–5.4 in Denmark, although there are few earthworms in soils of pH lower than 4.3, except for one species, *D. octaedra*, which seems to be very acid-tolerant (Bornebusch, 1930). Further evidence for the acid tolerance of *L. terrestris* comes from Vimmerstedt (1983) who introduced *L. terrestris* into a revegetated mine spoil with a pH of 3.5 in Ohio, USA, and reported that the earthworms became established on the spoil. *Eisenia fetida* has been reported to prefer soils with a pH between 7.0 and 8.0 (Rivero-Hernandez, 1991), but Edwards (1988) reported that it could tolerate a pH range from 4.0 to 7.0. Certain tropical species of *Megascolex* thrive in acid soils from pH 4.5 to 4.7 (Bachelier, 1963), and *Bimastos lonnbergi* is numerous in soils between pH 4.7 and 5.1 (Wherry, 1924). Baker and Whitby (2003a, b) reported strong aversion of *A. longa* in soils with pH 4.0 with little discrimination between pH 4.5 and 7.0 and slight aversion to soils above pH 7.0

Spiers et al. (1986) discussed an acid-tolerant earthworm species, *Arctiostrotus* sp., endemic to the organic horizons of coniferous podzols of Vancouver Island, Canada. These earthworms occurred in organic soil horizons with pH ranges from 2.6 to 6.2 and were most abundant at a site with a pH of 2.9. The authors concluded that these earthworms have a major role in the decomposer subsystem of these ecosystems, despite the extremely low pH prevailing at some sites.

Satchell (1955) considered that *Bimastos eiseni*, *D. octaedra*, and *D. rubida* were acid-tolerant species, and *A. caliginosa*, *A. nocturna*, *A. chlorotica*, *A. longa*, and *A. rosea* were acid intolerant (Fig. 7.7). He considered that *L. terrestris* was not very sensitive to pH, and Guild (1951) agreed with this conclusion, although Richardson (1938) considered that it was. Guild (1951) also confirmed that the relative abundance of *A. longa* and *A. caliginosa* was less in more acid soils. Madge (1969) reported that the optimum pH for *H. africanus* was between 5.6 and 9.2, so this species is somewhat acid tolerant. *Bimastos lonnbergi* and *B. beddardi* also seem to prefer acid soils (Wherry, 1924). An increase of pH from 7.25 to 8.25 was associated with a decrease in numbers of earthworms in 14 Egyptian soils studied by

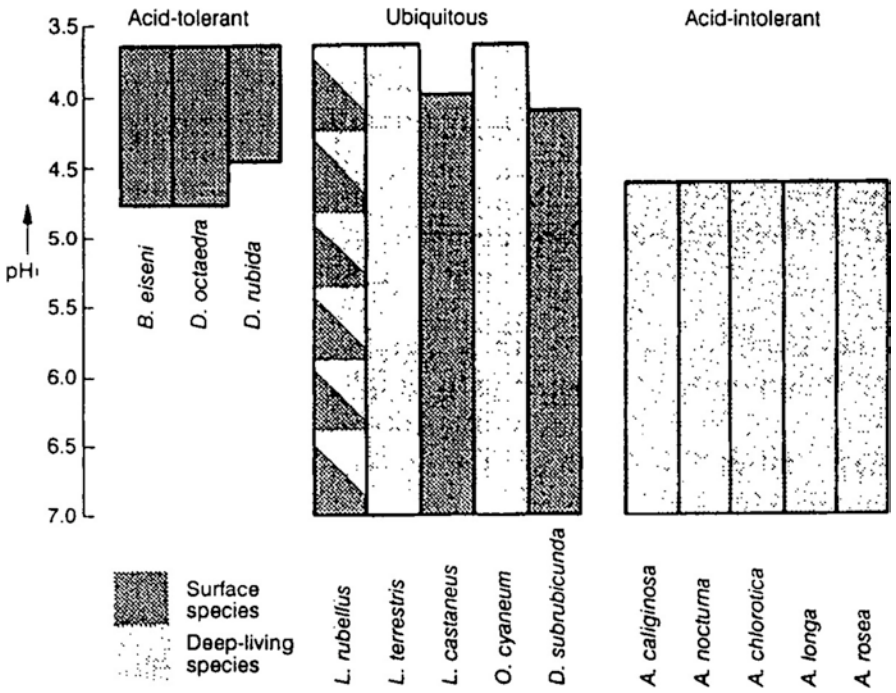

Fig. 7.7 Classification of earthworms as a function of the pH of litter (after Satchell, 1955)

El-Duweini and Ghabbour (1965a), demonstrating that soils can also be too alkaline to favor earthworms.

Bouché (1972) related the distribution of 67 taxa of Lumbricidae in France in relation to the pH of soil. Most species occurred in soils with a pH range of 7.0–7.4. Twenty-six acid-tolerant species were found in soils with a pH below 4.0 and 4 species were found only in soils with a pH above 6.6. The conclusion for European lumbricids is that most species have a wide range of tolerance for varying pH, some species being more acidophilic and others basophilic. The tolerance of earthworms in this wide range of pH values has been confirmed in recent studies by Eijsackers et al. (2005) who reported that the burrowing abilities of earthworms *A. caliginosa* were not affected by pH values of 5.8 and 6.5 in grassland and vineyard, respectively. In recultivated lignite-mined soils in Germany, a near-neutral pH earthworms counts ranged from 3 to 118 (Frund et al., 2004).

Satchell (1955) took soil samples from plots with long-term different fertilizer treatments, on a pasture experiment on Park Grass at Rothamsted. The pH values of the soils were 4.0, 4.1, 4.4, 5.0, 5.1, 5.6, 5.8, 6.9, and 7.0. He placed mature individuals of *A. chlorotica* on the surface of these soil samples and studied their reactions and the time they took to bury themselves. In the three most acid soils, worms at first showed a violent avoiding reaction, twisting, jerking convulsively, and

exuding coelomic fluid from their dorsal pores. They then extended to their full length and crawled about the soil surface, intermittently raising and waving the anterior segments. Activity gradually became sporadic, and after 1–2 h, they lay motionless and became flaccid. After 21 h, 58 out of 60 worms exposed to a pH below 4.4 were dead (Fig. 7.9).

Edwards and Lofty (1975) studied the populations of earthworms in the same Park Grass long-term fertilizer experiment in plots that had a range of pH from 3.7 to 7. They reported that *L. terrestris* became increasingly numerous as the pH increased, but most of the other species present, *A. nocturna*, *A. caliginosa*, *A. rosea*, *O. cyaneum*, tended to have an optimum pH range of 5.0–6.0. This agrees with the results of a study by Piearce (1972) who reported that, in a wide range of soils in North Wales, the number of species present and populations were greatest in soils with a pH of about 6.0 and least in soils with a pH below 5.0. Because soil pH is related to other soil factors that have an important influence on earthworm populations (e.g., clay content, cation exchange capacity), it is often difficult to establish a direct cause-and-effect relationship between soil pH and the size of earthworm populations, except in cases where earthworm populations are clearly inhibited by extremely high or extremely low hydrogen ion concentrations.

Reddy and Pasha (1993) reported a significant positive correlation between pH and the seasonal abundance of juvenile and young adult *Octochaetona phylloti* in semiarid tropical grassland in India, but the population of adult earthworms was affected more by rainfall than by pH. Staaf (1987) suggested that pH and factors related to pH were very important influences on the distribution and abundance of earthworms in acid beech forest soils in Sweden.

Chan and Mead (2003) reported a case study in the Southern Tablelands of New South Wales Australia where colonization of *A. trapezoides* as a function of soil acidity was investigated. Earthworm species distribution, abundance, and biomass were surveyed in a single dairy farm (238 ha) in Camden, New South Wales, Australia, and the results were related to a range of soil physical and chemical properties, namely, pH, texture, bulk density, soil organic carbon, and nutrient status. A 33.7-fold variation in total earthworm abundance (40–1347 m^{-2}) was found in the different fields of the single dairy farm, a magnitude of difference similar to those reported in regional surveys covering hundreds of square kilometers. The study showed that abundance of the earthworm was significantly related to the pH of the 0–10 cm soil layer with the following relationship after linear regression: abundance (m^{-2}) = 20.32*pH–81.39 (r = 0.79; $P < 0.001$, n = 32). This relationship decreases the earthworm population to zero at pH = 4. The study reported the significant effect of liming ($P < 0.02$) but not of tillage nor their interaction on the abundance of *A. trapezoides*. Addition of lime on the acid soil increased the abundance of this earthworm species. However, the latter was not affected by the different tillage practices. Population density of *A. trapezoides* on the limed plots averaged 6.3 times that of the unlimited plots (Table 7.4).

A. trapezoides has also been reported by Chan and Mead (2003) to be more sensitive to variation of pH values than the native earthworms below where pH was

Table 7.4 Abundance (number m^{-2}) of *A. trapezoides* and soil pH in the nil lime and limed soils under different tillage practices (Chan & Mead, 2003)

Lime (ton/ha)	Tillage	*A. trapezoides* (m^{-2})	pH
0	No-till	7.5 (12.9)	4.43 (0.69)
	One pass	0.0 (0.0)	3.97 (0.11)
	Conventional	1.9 (4.5)	4.04 (0.11)
4.4	No-till	13.0 (11.5)	4.84 (0.49)
	One pass	20.3 (24.7)	5.08 (0.35)
	Conventional	25.9 (28.6)	5.04 (0.46)

Numbers within parentheses are standard deviations

higher near tree stump and decreased with increasing distance away from a tree stump. More *A. trapezoids* congregated near a tree stump, and then populations decreased in distances away from the tree stump.

Soil pH may also influence the numbers of worms that go into diapause. Doeksen and van Wingerden (1964) reported that when they put individuals of *A. caliginosa* into soils with pH of 4.9, 5.4, 6.4, 7.6, or 8.6, the more acid the soil, the sooner worms went into diapause, and they remained in diapause longest in soil with a pH of 6.4.

It has been reported by several workers that earthworm casts are usually more neutral than the soil in which the worms live (Salisbury, 1925; Dotterweich, 1933; Puh, 1941; Stöckli, 1949; Finck, 1952; Nye, 1955; Sharpley & Syers, 1976; Reddy, 1983). One explanation suggested for this is that earthworms neutralize soil as it passes through their guts, by secretions of the calciferous glands. A more probable explanation is that the soil is neutralized by secretions from the intestine and by excretion of ammonia or that it is a combination of the two.

7.4 Aeration and Carbon Dioxide

There is little experimental evidence that the soil oxygen tension affects the distribution of earthworms in soil, although Satchell (1967) stated that the distribution of *B. eiseni* and *D. octaedra* appeared to be limited in some sites by the minimum oxygen tensions occurring at certain seasons; however, this was confused by factors such as pH, soil moisture content, amount of raw humus, plant cover, and soil microbial status. Satchell showed that there was some correlation between numbers of *B. eiseni* and oxidation-reduction potentials (E_h) of the soil. *Eisenia fetida* retreats from layers of organic matter when they become anaerobic (Edwards, 1988). In heathlands of Yorkshire, England, Satchell (1980) related extremely low numbers of earthworms in saturated depressions in the soil to the low E_h (174 mV) at these locations. Kaplan et al. (1980) showed that *E. fetida* could not survive in aged sewage sludge when the E_h was below 250 mV.

However, some earthworm species can survive for long periods at very low oxygen tensions. Not much is known of typical oxygen tensions that occur in soils, but Boynton and Compton (1944) reported that oxygen tensions in an orchard soil were below 10% for 11 weeks in the year at a depth of 90 cm, and for as long as 6 months at depths below 150 cm. Deep-burrowing species such as *L. terrestris* do not survive well in poorly drained soils that have low redox potentials below the surface horizons. More recent reports suggest that the depletion of oxygen due to prolonged flooding may eventually lead to the alteration of earthworm populations in the soil since different species have different tolerance level to low oxygen levels. Kiss et al. (2021a, b) reported that *L. terrestris*, a large species which emerges at night to forage at the soil surface died when oxygen levels reached 0.82 (±0.46) mg O_2 L^{-1} after approximately 36 h. *L. castaneus*, a smaller species which lives on the soil surface, died when oxygen levels reached 3.60 (±2.01) mg O_2 L^{-1} after approximately 168 h. *A. chlorotica*, which is similar in size to *L. castaneus*, lives in the upper 20 cm of soil and is known to aestivate during the summer, did not die, even when oxygen levels reached 1.49 (±0.40) mg O_2 L^{-1} after 280 h.

There is little evidence of the vertical distribution of earthworms being affected by CO_2 concentrations in soil, and the worms do not seem to migrate in response to high CO_2 concentrations. For example, *E. fetida* did not respond to soil concentrations of CO_2 up to 25% (Shiraishi, 1954). The limits of CO_2 concentration in soil are normally between 0.01% and 11.5%, and earthworms can survive much greater concentrations than this, even up to 50% (Russell, 1950; Chap. 4).

Zaller and Arnone (1999) hypothesized that elevated concentrations of atmospheric CO_2 in the soil will increase the activity of earthworms via production of surface castings due to increase in C supply that will consequently increase plant litter production and increased water contents. This hypothesis was tested on a calcareous grassland under elevated CO_2 conditions. Using a screen-aided CO2 control facility (open top and open bottom rings), eight 1.2 m^2 grassland plots in Switzerland have been maintained since March 1994 at ambient CO^2 concentrations (350 µl CO_2 l^{-1}) and eight at elevated CO_2 (610 µl CO_2 l^{-1}) for 1 year. It was reported that earthworm cast production under elevated CO_2 concentrations was 35% greater ($P < 0.05$) than under ambient CO_2 concentrations. The increases in cast production also significantly increased (30%) total N and organic C in the soil. However, seasonality of earthworm activity has no correlations with the concentrations of CO_2.

7.5 Soil Type

Earthworms are influenced by soil type and texture, although there have been relatively few studies of the direct influence of soil type on earthworm populations. Guild (1948, 1951) made a survey of the main soil types in Scotland and reported that there were differences both in total numbers and relative numbers of each species in soils of different textural composition (Fig. 7.8, Table 7.5). Light and medium

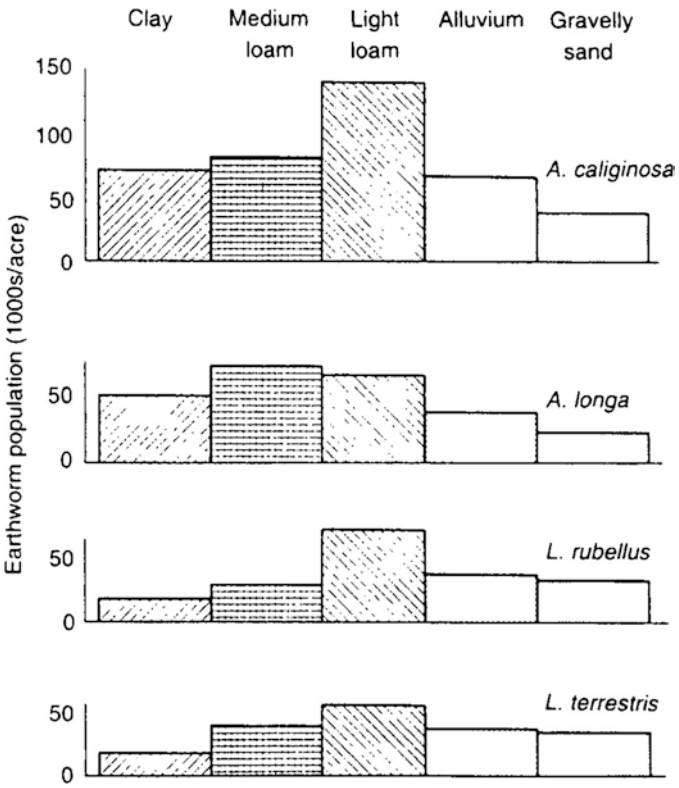

Fig. 7.8 Density of earthworm populations (thousands/ha) in various soil types in Scotland (adapted from Guild, 1948)

Table 7.5 Relations of soil type to earthworm populations

	Population		
Soil type	Thousands/ha	No./m^2	No. of species
Light sandy	232.2	57	10
Gravelly loam	146.8	36	9
Light loam	256.8	63	8
Medium loam	226.1	56	9
Clay	163.8	40	9
Alluvium	179.8	44	9
Peaty acid soil	56.6	14	6
Shallow acid peat	24.6	6	5

From Guild (1951)

loams had greater total populations of worms than heavier clays or more open gravelly sands and alluvial soils. *Allolobophora caliginosa* was the dominant species in all soil types, and *A. longa* was less important in open soils, gravelly sands and alluvial soils. In a survey of the distribution of earthworm species in the Hebrides, Boyd (1957) compared the relative abundance of earthworm species in light soils with those in calcareous sand and dark peaty soils. Six species were more abundant on the light soils and six on the dark ones. In particular, *A. caliginosa* and *L. castaneus* were much more numerous in the light soils, and *B. eiseni* and *D. octaedra* in the dark soils. A few small species of earthworms can survive in deserts and semideserts (Kubiena, 1953; Kollmannsperger, 1956), and some worms can inhabit the arid, cold soil of northeastern Russia. Deep-burrowing anecic species such as *L. terrestris* require adequate soil depth to build their burrows and do not thrive in shallow soils (Piearce, 1978; Muys et al., 1992).

El-Duweini and Ghabbour (1965a) showed that populations of *A. caliginosa* in Egypt decreased with increasing proportions of gravel and sand in soils. This relationship did not hold in soils that had higher water contents, indicating that some of the effects of texture were due to its influence on soil moisture. In the forest, pasture, and heathlands in Sweden, Nordström and Rundgren (1974) found a significant positive correlation between earthworm abundance and soil clay content in soils that were categorized as having 0–5%, 5–15%, or 15–25% clay. In particular, populations of *A. caliginosa*, *A. longa*, *A. rosea*, and *L. terrestris* were correlated positively with clay content at 0–60 cm.

Hendrix et al. (1992) studied the distribution of earthworms at sites representing various ecosystem types, management practices, landscape positions, soil texture, and soil erosion status on the Georgia Piedmont in southeastern USA. Moderately and severely eroded sandy clay loams supported significantly more earthworms and greater biomass than slightly eroded soil with a higher sand content. Of the soil texture variables, the silt content of the soil was correlated most with earthworm abundance. These results may have been due to the lower organic matter content and water-holding capacity of the sandy soils.

In their investigation of the diversity and abundance of earthworms in pasture soils at 113 sites in South Australia, Baker et al. (1992) found weak positive correlations between clay content of the soil and the abundance of *A. trapezoides*, *A. rosea*, and *A. caliginosa*. Of these three species, *A. caliginosa* exhibited the strongest positive correlation with clay content. The numbers and weights of *A. caliginosa* and *A. trapezoides* were correlated negatively with the sand content of the soil.

Sveistrup et al. (1997) reported differences in earthworm activities determined by the presence of channels in three areas (Landvik, Voll and Kvithamar) with distinct soil types: cultivated loamy (Humic Cryaquept) and clayey (Typic Endoaqualf and Typic Cryaquept) located in Southern and Northern Norway. Four species of earthworms were found: *A. caliginosa*, *A. rosea*, *A. chlorotica*, and *L. rubellus*. At Landvik (loamy), *A. caliginosa* and *L. terrestris* dominated, with medium (4–6 mm) and coarse (>6 mm) channels found most numerous below the plough layer. No coarse channels were found in clay sites (Voll and Kvithamar). The volume of

earthworm channels below the plough layer was 0.6–0.8% of the soil volume at Landvik and Voll and 0.3–0.4% at Kvithamar.

Bulk density was one of the soil properties that has been reported by Rossi (2003) to have an influence on the spatiotempopral distribution of tropical earthworms. The abundance of earthworm species was estimated on five occasions covering 2 years within a single plot sampled with 100 sampling locations. The results showed that the earthworm community was highly structured in space and that the spatial pattern was stable through time. The spatial distribution of soil bulk density was highly correlated with the earthworm community structure. Clumps of eudrilid species correspond to areas of lower soil bulk density, whereas patches of *M. anomala* fit with areas of higher bulk density. *D. agilis* is an epigeic species and therefore has less effect on soil structure. Lapied et al. (2009) reported clear preference of some earthworm species on soil types. A field experiment was duplicated on a clay loam and a sandy loam soil in the Saint-Lawrence Valley. Both sites were enriched with urban compost or mineral amendment. The effects of amendments on soil properties and the earthworm community were evaluated by uni- and multivariate analyses at two soil depths (0–10 and 10–20 cm) and after two growth seasons. Compost-amended plots had higher pH, wet aggregates stability, total N and C, OM, K, and Ca in the 0–10 cm soil layer than plots receiving mineral fertilizer. Two endogeic species, *Aporrectodea caliginosa* and *Allolobophora chlorotica* were dominant in both sites. Other species were all epigeic and were rare. Abundance and biomass of earthworms (0–10 cm) were significantly higher in clay loam, with a similar proportion in *A. caliginosa* (263 ind m^{-2}) and *A. chlorotica* (228 ind m^{-2}). In sandy loam, *A. caliginosa* was the most abundant (18 ind m^{-2}), *A. chlorotica* was scarce (1.3 ind m^{-2}), and epigeic species were absent. The density and biomass of earthworms were significantly higher with compost amendment, up to 12 times in clay loam: *A. chlorotica* reached a mean density of 420 ind m^{-2} vs. 36 ind m^{-2} with mineral amendments, *A. caliginosa* 344 ind m^{-2} vs. 183 ind m^{-2} and epigeic earthworms 19 ind m^{-2} vs. 12 ind m^{-2}. Significantly more earthworms and higher diversity (presence of epigeic species) were encountered in the clay loam site, which can be directly related to the general preference of earthworms for fine-textured soils (Edwards & Bohlen, 1996; Fraser, 1996; Baker et al., 1998)

Soil texture can influence earthworm populations because of its effects on other soil properties such as soil moisture relationships, nutrient status, and cation exchange capacity, all of which can have important influences on earthworm populations. In an analysis of earthworm communities of tropical rainforests, Fragoso and Lavelle (1992) showed that earthworm communities dominated by geophagous species are characteristic of nutrient-rich soils, whereas those dominated by litter feeding, epigeic species are normally present in nutrient-poor soils. They showed that the percentage dominance of epigeic species in the earthworm community was negatively correlated with the amounts of calcium, magnesium, and nitrogen in the soil.

In laboratory conditions, Baker and Whitby (2003a, b) reported that a commercially available mixture of sand/loam supplemented with sheep dung favored the growth of *A. longa* over those mixtures without sheep dung as a source of earthworm food.

7.6 Organic Matter

The distribution of organic matter in soil influences the distribution of earthworms greatly. High-quality organic matter supports earthworm population favorably (Cesarz et al., 2013). Soils that are poor in organic matter do not usually support large numbers of earthworms. Conversely, if there are few earthworms, the decaying organic matter usually lies in a thick mat on the soil surface. Such mats of undisturbed organic matter occur in both woodlands (Richardson, 1938) and grassland (Raw, 1962). In irrigated pastures in New South Wales, Australia, that contained no earthworms, such mats of organic matter were up to 4 cm thick until earthworms were introduced experimentally (Stockdill, 1966).

Some species of earthworms are attracted readily to animal droppings and dung on the soil surface. In experiments at Rothamsted, which compared plots to which dung was added annually with plots which were left unmanured, large differences in earthworm populations were noted (Fig. 7.9). Plots that grew wheat regularly for many years had earthworm populations that were three to four times greater in plots receiving 35 tons/ha of dung than in unmanured plots (Table 7.6). The numbers in Park Grass at Rothamsted, a long-term pasture fertilizer experiment, were three times greater in plots receiving 3 tons/ha of dung than in unmanured plots after 140 years. In Barnfield, in a fertilizer experiment in an arable field growing continual mangolds, there were about 15 times more earthworms in plots receiving dung annually than in unmanured plots after 130 years (Table 7.4). In Sweden, Nordström and Rundgren (1974) found significant correlations between the organic matter content and clay content of soils and the abundance of deep-burrowing species of earthworms. Large amounts of dead roots and other organic matter in pasture usually coincide with large numbers of earthworms, and it is probably the gradual decrease in soil organic matter, when pasture is ploughed and used for arable crops, which leads to a corresponding decrease in earthworm populations.

Decaying leaves in woodlands are also a source of organic matter that usually favors earthworm multiplication. Earthworms can remove a large part of the annual leaf fall in a woodland or orchard if populations are large and the leaf litter is of a species that is palatable to the worms present.

Several workers have reported strong positive correlations between earthworm numbers and biomass and the organic matter content of the soil. Increases in the organic carbon content of semiarid agricultural soils in Egypt were associated with increased numbers and biomass of earthworms (El-Duweini & Ghabbour, 1965a; Ghabbour & Shakir, 1982). Hendrix et al. (1992) reported a strong positive correlation between earthworm population density and soil organic matter content across ten sites, which included conventional and no-tillage agroecosystems, grass meadows, and a mixed deciduous forest, in the southeastern USA. There is little doubt that the availability of organic matter is one of the most important factors influencing earthworm abundance.

Van Vliet et al. (2007) reported strong positive correlations between organic matter content of soil and the abundance of earthworms. They selected two grasslands

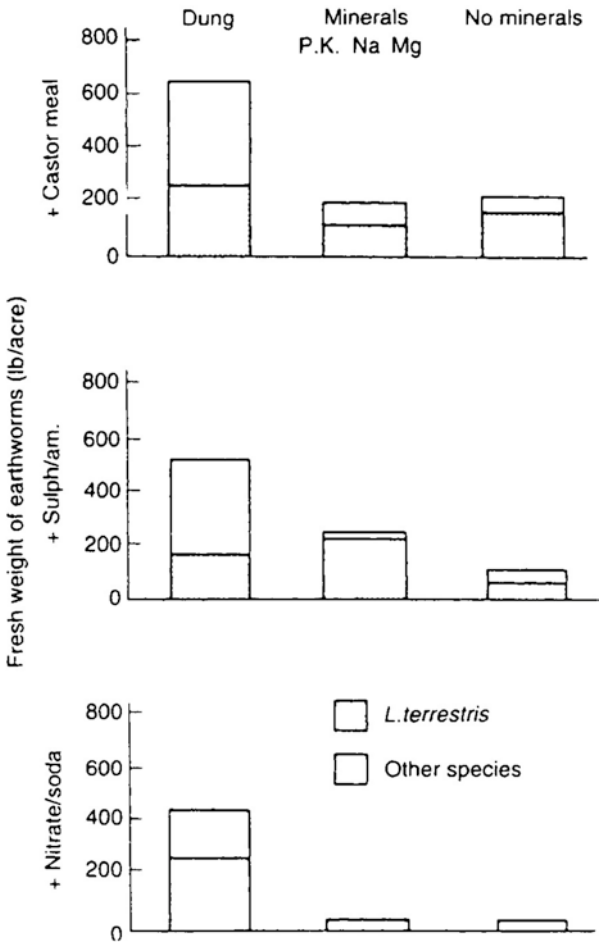

Fig. 7.9 Earthworm populations (kg/ha) in an old arable field (Barnfield, mangolds) (Edwards and Lofty, 1977).

differing in organic matter content at nine dairy farms on sandy soils in the Noordelijke Friese Wouden (NFW) in the Netherlands. At each farm, the grassland with the highest organic matter content contained the largest number of earthworms (up to 858 worms m^{-2}), (r = 0.286 (p = 0.036)). These grasslands also had the highest root biomass (r = 0.504 (p = 0.0001). With an increase in organic matter in the soil (from 5% to 10.2%), potential nitrogen mineralization increased from 138 to 310 kg N^{-1} ha 6 $months^{-1}$.

Araujo and Lopez-Hernandez (1999) reported increases in earthworm populations from 1.6% to 4.8% greater after additions of organic fertilizers in agroforestry systems (AFS) established for a period of 25 years compared to original natural savanna (NS) soils in Venezuelan Ammozonia. Positive correlations of the abundance of earthworms and plant litter decomposition in riparian and upland within wet tropical forests in Puerto Rico were reported by Dechaine et al. (2005).

Table 7.6 Earthworm populations in plots with and without dung

	1. Grassland Park Grass, Rothamsted (Satchell, 1955)		2. Arable land Barnfield, Rothamsted (Edwards and Lofty, 1977)	
Species	Unmanured	Dung	Unmanured	Dung
L. terrestris	13.1	22.5	0.23	10:8
L. castaneus	16.0	59.6	–	–
A. caliginosa	2.9	8.0	0.8	15.4
A. chlorotica	1.6	–	3.2	44.6
A. rosea	10.0	21.3	–	0.23
A. longa	–	–	0.46	1.8
A. nocturna	1.3	18.9	–	–
O. cyaneum	6.9	24.5	–	–
Total	51.8	154.8	4.69	72.83

Biochar, a different form of organic matter, has gained popularity in the last decade as a soil amendment that has been reported to influence crop growth positively and enhance some soil properties favoring soil microbial populations (Zhang et al., 2015; Baiamonte et al., 2019). Whalen et al. (2021) conducted a study to assess earthworm population in biochar-amended soils on a dairy farm in St. Francis River watershed, Quebec, Canada. The study concluded that biochar and dairy slurry applied at rates of 5 and 10 t ha^{-1} did not affect the earthworm populations composed of *Aporrectodea turgida*, *Aporrectodea tuberculata*, and *Lumbricus rubellus*. Ferreira et al. (2021) utilized an endogeic cosmopolitan species *Pontoscolex corethrurus* in a standard ecotoxicological laboratory trial to assess the impact of Brazil-nut husk biochar application (0, 2.5, 5, and 10% w/w). The study reported that biochar addition up to 10% w/w had no negative effects on *P. corethrurus*, and ingested biochar particles showed signs of physical degradation and bacterial colonization

7.7 Food Supply

Earthworms can use a wide variety of organic materials for food and even in adverse conditions can extract sufficient nourishment from organic matter and microorganisms in soil to survive. The kind and amount of food available influence not only the size of earthworm populations but also the species present, and their rate of growth and fecundity. Evans and Guild (1948) investigated the influence of food on earthworm cocoon production (Table 7.7) and showed clearly that more cocoons were produced by worms that were provided with decaying animal organic matter, than by those provided with fresh plant material. They also showed that earthworms fed on any nitrogen-rich diets grew faster and produced more cocoons than those with little nitrogen available. Barley (1959) provided individuals of *A. caliginosa* with

Table 7.7 Mean number of cocoons produced by five earthworms in 3 months

Food	*A. chlorotica*	*L. castaneus*
Fodder	0.8	9.4
Oat straw	1.4	12.0
Bullock droppings	12.4	73.2
Sheep droppings	14.0	76.0

From Evans and Guild (1948)

Table 7.8 Changes in body weight of *A. caliginosa* when fed for 40 days on various diets

Food	% change in weight
Angaston soil	−53
Phalaris roots	−26
Phalaris leaves	−26
Clover roots	−2
Clover leaves	+18
Dung, on surface	+71
Dung, incorporated	+111

From Barley (1959a)

different diets and reported that they grew at very different rates on these diets, growing fastest when provided with animal dung (Table 7.8).

Boström and Lofs-Holmin (1986) reported that the growth of *A. caliginosa* depended not only on the type of food available but also on the particle size of the food material. Earthworms grew best with shoots of meadow fescue, followed by provision of alfalfa shoots and roots. Earthworms provided with barley straw fragments smaller than 0.2 mm gained more than twice as much weight during 150 days as earthworms provided with fragments ranging from 0.2 to 1.0 mm in size, indicating the importance of food particle size to the nutritional quality of food material.

Guild (1955) stated that most species of earthworms prefer dung or succulent herbage to tree leaves and that pine needles are preferred least of all; Barley (1959) corroborated this conclusion for *A. caliginosa*. Guild (1955) estimated that mature individuals of *A. longa* can ingest 35–40 g dry weight of dung per annum, *A. caliginosa* 20–24 g and *L. rubellus* 16–20 g.

Svendsen (1957b) reported that, whereas individuals of the pigmented species *L. festivus*, *L rubellus*, *L. castaneus*, *D. octaedra*, *D. rubida*, and *B. eiseni* became aggregated in dung, those of the unpigmented, geophagous species *O. cyaneum*, *O. lacteum*, *A. caliginosa*, *A. chlorotica*, *A. longa*, *A. rosea*, and *E. tetraedra* f. *typica* did not. Earthworms of the species *A. rosea* and *A. caliginosa* are not attracted to leaf litter (Lindquist, 1941) but readily eat dung, and *A. caliginosa* and *L. rubellus* will also feed on dead root tissues in pasture (Piearce, 1978). Müller (1950)

considered that *A. caliginosa* fed extensively on fungal mycelia, but it seems that this species tends to be omnivorous. Individuals of *A. caliginosa* do not eat fallen leaves until these have become moist and brown (Barley, 1959), and they cannot maintain their body weight on dead roots, which tends to discount Waters' (1955) claim that dead roots are the main diet of this species.

An examination of the diets and gut contents of *A. caliginosa* and *L. rubellus* in a deciduous woodland suggested that *L. rubellus* is primarily a litter feeder, whereas *A. caliginosa* consumes organic matter in a more advanced state of decomposition. The material ingested by *L. rubellus* was richer in calcium than that consumed by *A. caliginosa*, and the former species has a mechanism for excreting calcium (Piearce, 1972). Piearce (1978) examined the gut contents of six species of Lumbricidae in a pasture in North Wales, UK, and identified different ecological groups of worms based on gut contents and feeding behavior. *Lumbricus castaneus* and *L. rubellus* consumed material rich in relatively undecomposed plant remains, whereas *A. caliginosa* and *A. chlorotica* fed mainly on well-decomposed organic detritus; *A. longa* and D. *mammalis* were intermediate in their dietary requirements.

Doube et al. (1997) examined food preferences of Lumbricid earthworms where a circular choice chamber containing 18 feeding stations was used to assess the food-type preference of four earthworm species (*A.* caliginosa, *A. longa*, *L. rubellus*, *L. terrestris*). Four types of organic matter were used: cow dung, sheep dung, decomposed leaf litter, and sewage sludge, introduced either alone or mixed in sandy loam soil or soil alone. All earthworms showed a strong preference for pure mineral soil over pure organic matter. Also, mineral-organic mixtures were clearly preferred to pure organic sources, with leaf litter + soil being the preferred mixture for all four earthworm species tested. In addition, cow ding + soil and sewage +soil were acceptable to all species except *A. caliginosa*. It appeared that mineral soil enhanced the palatability of the organic food sources used in the experiment (Figs. 7.10, 7.11, 7.12 and 7.13).

The different preferences of earthworms to different animal dung were reported in a study by Scown and Baker (2006) in pasture lands of southeastern Australia. The attractiveness of dung from sheep, cattle, and horses was measured by determining the abundance and biomass of the resident earthworm species under each dung type at varying times after adding the dung to the soil surface (0, 10, 20, and 30 days). The earthworm population consisted of three exotic species, *Aporrectodea trapezoides*, *Microscolex dubius*, and *M. phosphoreus*, and two native species, *Spenceriella macleayi* and *S. bywongensis*. Both the number of days that the dung was available to earthworms and the type of dung influenced the numbers and biomass of the earthworms found beneath the dung pats. Significant interactions existed between time and dung type when all adult earthworms were considered as one group and also when adults were split into individual species. The various species responded differently to the dung, but horse dung was generally the more preferred dung type.

The management of organic matter soils planted with annual crops such as tomatoes showed to strongly influence the population dynamic of earthworms. This condition was particularly observed and reported by Fonte et al. (2009) after surveying

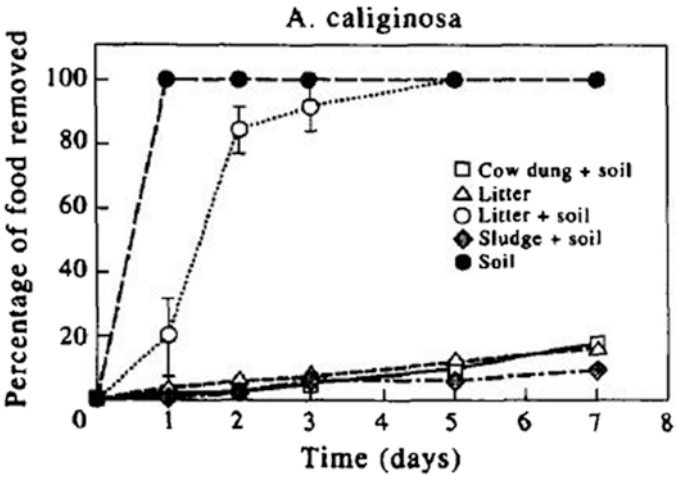

Fig. 7.10 Food preference *A. caliginosa*. Rate of food removal shown as a percentage (± SE of the mean) and absence of error bar indicate a very small SEM

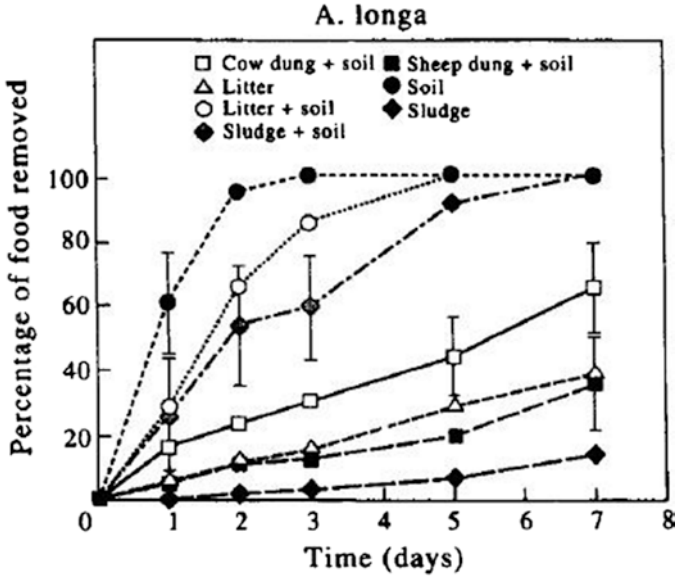

Fig. 7.11 Food preference A. longa. Rate of food removal shown as a percentage (± SE of the mean) and absence of error bar indicate a very small SEM

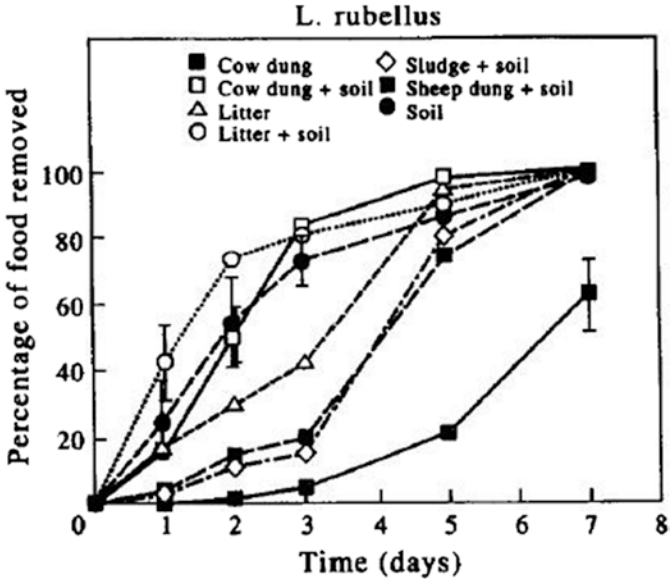

Fig. 7.12 Food preference *L. rubellus*. Rate of food removal shown as a percentage (± SE of the mean) and absence of error bar indicate a very small SEM

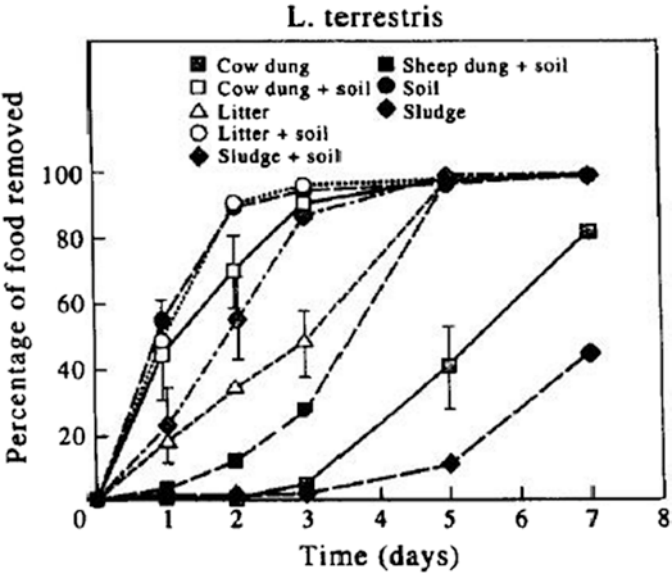

Fig. 7.13 Food preference *L. terrestris*. Rate of food removal shown as a percentage (± SE of the mean) and absence of error bar indicate a very small SEM.

earthworms on 16 areas of tomato cropping systems. The earthworms identified in this survey were composed entirely of exotic species and were dominated by *Aporrectodea caliginosa*. Earthworm abundance was related to residue management, with the tomato mulch systems averaging 4.5 times greater fresh earthworm biomass than bare fallow ($P = 0.024$).

Most species of earthworms can distinguish between different kinds of forest litter. Darwin (1881) claimed that earthworms showed preference for leaves of particular shapes, but Satchell (1967) found that there was an order of preference for certain leaf species, if uniform disks of a range of species of leaves were offered. Gast (1937) ascribed this preference to the mineral content of certain species of leaves, but this has not been confirmed. Mangold (1951) believed that some species of leaves were unattractive to earthworms because of their bitter alkaloid or noxious aromatic content. Litter rich in protein is accepted more readily than deficient in protein (Wittich, 1953), but protein content is often correlated with sugar content (Mangold, 1953; Laverack, 1960), which may also be more important. Edwards and Heath (1963) buried leaf disks in nylon bags made from mesh with 7.0 mm apertures, so that *L. terrestris* could feed on them, and found that oak disks were preferred to beech, and in another experiment (Heath et al., 1966) stated that the order of preference for a range of different species of leaves buried in similar mesh bags was lettuce, kale, beet, elm, maize, lime, birch, oak, and beech.

Leaves of larch, spruce, oak, and beech, which are all comparatively unpalatable to earthworms, contain condensed tannins that are not found in dog's mercury, nettle, elderberry, ash, and wych elm, all of which are more palatable (Brown et al., 1963). King and Heath (1967) reported that the amount of water-soluble polyphenols in litter was inversely proportional to the rate at which it was consumed, and that litter became much more palatable after a few weeks of weathering. In a study of the palatability of litter to individuals of *L. terrestris*, Satchell (1967) showed that there was an inverse correlation between the palatability of litter and its total polyhydric phenol content and a positive correlation with the amount of soluble carbohydrates. Edwards and Lofty (1977) showed that the palatability of oak and beech leaves could be increased by washing out water-soluble polyphenols. Such observations help to explain why the leaves of certain species of trees disappear from the soil surface faster than others and become broken down and incorporated into soil more readily. Other choice experiments have shown that leaf litter with low C:N ratio and low concentrations of secondary compounds and polyphenol content are much preferred by earthworms (Rajapaksha et al., 2013; Liebeke et al., 2015)

Huerta et al. (2005) reported enhanced reproduction of tropical earthworm *Polypheretima elongata* after additions of *Zea mays* and *Mucuna pruriens* into earthworm cultures in the laboratory. The highest individual fresh weight (5.8 ± 0.7 g after 63 days) and the highest cocoon production (33 ± 8.4 cocoons ind^{-1} in 98 days) were obtained when litter of *M. pruriens* var. *utilis* were added to the soil. *Mucuna* leaf material was more efficient when fresh, whereas maize litter gave higher growth and fecundity rates when composted for 6 weeks. Hendriksen (1990) used litter bags in experiments with ten different types of litter in a pasture and observed that detritivore earthworm species (*Lumbricus* spp.) preferred ash,

basswood, and predecomposed elm and beech litter to undecomposed beech litter. The numbers of litter feeding earthworms found beneath the litter bags were correlated negatively with the C:N ratio and final polyphenol concentration of the litter. In mulching experiments with five types of plant residues in the humid tropics, Tian et al. (1993) reported that earthworm populations were negatively correlated with the ratio of lignin to nitrogen of the plant residues. Litter quality indices such as N, P, Ca, and Mg concentrations showed to positively affect the growth of earthworms *A. caliginosa* and *O. tyrtaeum*. This was shown by Cesarz et al. (2016) that showed increased in mass gained by earthworms in microcosm experiment with soils containing higher quality litter composed of incubated mixture of litters from tree species of Central Europe (*Fagus sylvatica*, *Acer platanoides*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia* spp., and *Fraxinus excelsior*). The experiment further showed that leaf litter quality had a more significant effect on the mass gain of these endogeic earthworms that soil quality parameters considered, i.e., pH, C, and N.

Other factors also influence the palatability of leaves to earthworms. Starved worms will consume leaves of species that they would normally reject. Addition of bacterial cells to leaves increased their acceptability (Wright, 1972). Many chemicals, such as pesticides, can render normally palatable leaves unpalatable. The addition of *Pseudomonas corrugata* 2140R *lux* 8 to 9 types of food in the feeding trial conducted by Doube et al. (1997) did not seem to have any influence on the preferences of earthworms to these food. However, the experiment did not include a group that was not inoculated with this bacteria at all. Although overall microbial biomass can be positively increased by leaf litter quality, it is not necessarily a predictor of increased earthworm growth (Cesarz et al., 2016). Still other reports suggest the importance of microorganisms, mainly fungi, for nutrition and as helpers for further food degradation when ingested (Curry & Schmidt, 2007).

Vegetation can affect earthworm populations by altering the quantity and quality of their food supply. Phillipson et al. (1976) showed a strong positive association between numbers of *A. caliginosa* and eight species of ground flora in a beechwood in England. They suggested that the ground flora may have provided important food resources to the worms in the form of dead roots and microorganisms associated with the decaying roots. Populations of *Pontoscolex corethrurus* and *Amynthas gracilis* were influenced strongly by tree species in tropical tree plantations in Hawaii (Zou, 1993). The population density of worms ranged from 92 per m^2 in pure *Eucalyptus* stands, 281 per m^2 in mixed *Eucalyptus-Albizia* stands (25% *Albizia* and 75% *Eucalyptus)* and 469 per m^2 in pure *Albizia* stands. Although *Eucalyptus* trees produced more litter, *Albizia* trees produced more fine litterfall and earthworm densities were correlated positively with the nitrogen content and concentration of fine litterfall. Boettcher and Kalisz (1991), working in forests in eastern Kentucky, USA, showed that earthworm populations were significantly lower under yellow poplar (*Liriodendron tulipifera*) and eastern hemlock (*Tsuga canadensis*) when rhododendron (*Rhododendron maxima*) was present in the understory than when it was not present. The effect of rhododendrons on the mineral soil in which they grow affected both the abundance and species composition of earthworms in the soil.

Vegetation in urban environments can influence the population of earthworm species composition and population (Xie et al., 2018; Moore et al., 2017). Bajcz et al. (2018) reported that non-native earthworm densities correlate with aboveground plant biomass and vegetation type, prairie gardens, and turfgrass, across residential properties in Madison, Wisconsin. They found that earthworm densities increased by 0.1 and 2.7 individuals m^{-2} on average with each increase of 1 gm^{-2} in standing plant biomass and of 1% in soil moisture, respectively. Further, when the effects of plant biomass and soil moisture were factored out, earthworm densities were estimated to be 55 individuals m^{-2} lower in prairie gardens than in adjacent lawns (Bajcz et al., 2018).

Other evidence for the influences of different tree species on earthworm communities comes from Muys et al. (1992), who showed that earthworm communities differed considerably on grassland sites in Belgium that were afforested with different tree species. Earthworm biomass diminished under oak (*Quercus palustris*) stands due to poor quality of the oak litter and acidification of the soil by oak leaves.

There have been several different estimates of the amounts of food taken by earthworms and passed through their guts, but there is good agreement between different workers. Guild (1955) calculated that worms of 0.1 g body weight eat as much as 80 mg of food/day/g of body weight of worms. Satchell (1967) calculated that individuals of *L. terrestris* pass between 100 and 120 mg/g/day through their guts, and Crossley et al. (1971) calculated that a species of *Octolasion* had a soil intake of 1.2% of its live body weight per hour, which equals about 29% of its body weight per day or 290 mg/g/day. Barley (1959a) calculated that *A. caliginosa* consumed 200–300 mg/g/day.

7.8 Interactions Between Environmental Factors

There have been relatively few studies which assessed how interactions between environmental factors influence earthworms. Clearly, temperature and moisture are usually inversely correlated, and it is often difficult to separate their effects. Similarly, it is difficult to separate the effects of soil organic matter content from the availability of decaying plant material as food. However, Briones et al. (1992) reported that a group of species, *A. caliginosa*, *D. mammalis*, *L. rubellus*, *E. tetraedra*, and *D. rubida*, could be separated from *A. rosea* and *A. chlorotica* by combined preferences for organic matter, soil texture, and moisture content. Al-Maliki et al. (2021) summarized the impact of temperature and soil moisture on earthworm species abundance and biomass, earthworm populations, and earthworm activity in various ecosystems in Table 7.9. Their comprehensive review showed that less fatal temperatures are generally unknown, but higher fatal temperatures range from 25 to 48 °C; improvements in microbial biomass and plant growth have been established according to temperature, soil toxicity, soil type, earthworms abundance, organic residues types, and field conditions; and although the summer temperature in the arid area was approximately 48°C, it was found that a particular type of earthworm (*Namalycastis indica*) was responsible for improving soil characteristics.

Table 7.9 Impact of temperature and soil moisture on earthworm species abundance and biomass, earthworm populations, and earthworm activity in various ecosystems

Earthworm species	Region	Temperature	Soil moisture	Earthworm activity	References
Lumbricus terrestris	UK	15–20 °C	21%	Improved soil structure, biomass carbon	Al-Maliki and Scullion (2013)
Eisenia fetida	UK	10 °C	18%	Minimized feeding activity	Satchell (1967)
Lumbricus terrestris	UK	15–20 °C	20%	Improved soluble carbon, fungal length and soil structure	Al-Maliki et al. (2017)
Eisenia fetida	UK	25–30 °C	22%	Enhanced feeding activity	Satchell (1967)
Amynthas corticis Aporrectodea caliginosa, *Dendrodrilus rubidus Helodrilus oculatus*	Qatar	20–35 °C	14%	Improved soil fertility	Al-yousuf and Hagras (1986)
Namalycastis indica	Iraq	20–48 °C	12%	Improved soil quality	Al and Altaee (2011)
Lumbricus terrestris	Iraq	40 °C	13%	Decreased soil burrowing capability under pesticide application	Farman (2014)
Aporrectodea caliginosa	Qatar	25 °C	15%	Accumulated high levels of insecticides in their bodies, thus enhanced soil quality	Al-yousuf (1995)
Eisenia fetida	UK	Below 10 °C	22%	limited feeding activity	Edwards and Bohlen (1996)
Dendrobaena octaedra	UK	6 °C	11%	Dry summers had negative effects on epigeic species	Eggleton et al. (2009)
Amynthas agrestis	USA	−5, and 35 °C	24% and 54%	The survival of earthworm in soils at −5, 5 or 35 °C was not observed at any level of soil moisture	Richardson et al. (2009)
Aporrectodea tuberculata	Canada	5, 10, 15, and 20 °C	10, 15, 20, and 25%, dry weight basis	In incubated soil with 25% moisture at 15 and 20 °C, earthworm weight was increased. Lowest survival at soil moisture levels below 10%	Wever et al. (2001)

From Al-Maliki et al. (2021)

Observations of the dynamics of earthworm populations and abundance have been noted recently in perturbed systems, such as in urban areas, where interactions of environmental factors can take place. Xie et al. (2018) reported that urbanization decreases earthworm abundance and biomass where soil moisture and pH as the most important edaphic variables. It was also reported the abundance of earthworms was negatively correlated with the soil organic C. Talavera et al. (2020) evaluated the richness and composition of species in relation to environmental and anthropogenic characteristics, including soil properties, altitude, land-use intensity or distance to urban nuclei in São Miguel Island (Azores, Portugal). Results suggested that land-use intensity, represented as five categories ranging from undisturbed sites with native vegetation to sites under intensive agriculture exploitation, is a good predictor of species composition. Their study demonstrated that soil pH affected the establishment of species and that organic matter is positively associated with abundance of some non-native lumbricids (e.g., the anecic *Octodrilus complanatus* Dugés, 1828) and negatively related to richness and abundance of exotic species such as *Amynthas corticis*, *Amynthas gracilis* Kingberg, 1867, and *Pontoscolex corethrurus* Müller, 1857.

In temperate grasslands of Brittany, France, Hoeffner et al. (2021) evaluated the effects of soil properties (texture, organic matter content, and pH), grassland management (grassland age, livestock unit, and type of fertilization), landscape diversity (richness, diversity of surrounding habitats, and grassland plant diversity), and the presence of hedgerows on the assembly of earthworm communities. The study showed that increase in soil organic matter content and pH were the most favorable factors for earthworm abundance and biomass, in particular for endogeic species; the increase in the livestock unit was the most damaging factor for earthworm communities, in particular for the anecic earthworm biomass and endogeic species richness, and landscape diversity negatively affected the total earthworm abundance and epigeic earthworm biomass, but it was related to an increase in the epi-anecic species. In agroecosystems with forested riparian strips, Cameron et al. (2021) found that earthworms were more abundant in forested riparian strips than in fields in Cana, while the opposite pattern was observed in Central Europe. Differences were attributed to rainfall patterns with overall positive relationships between earthworms and soil clay content, pH, moisture, and organic matter was observed.

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